

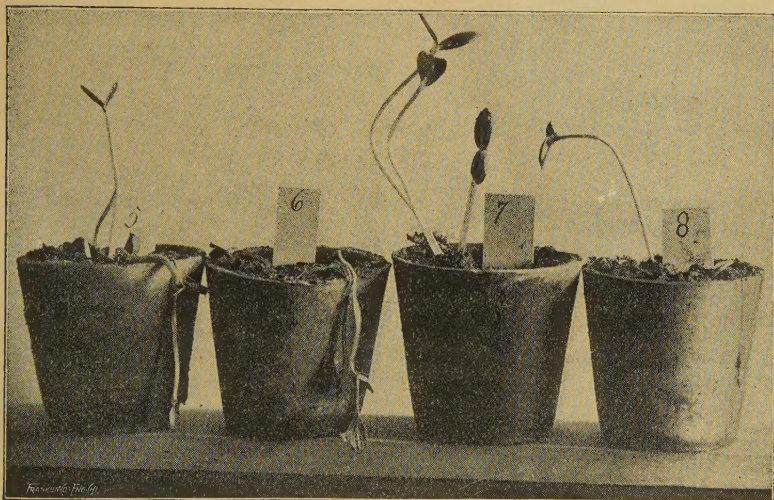
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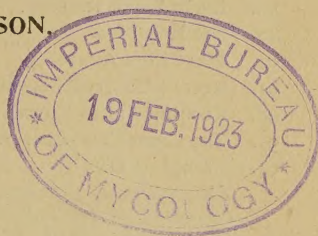
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Cornell University Agricultural Experiment Station,
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DAMPING OFF.



By GEO. F. ATKINSON.



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DAMPING OFF.

"Damping off" is a disease of seedling plants which rots or disintegrates the tissues at the surface of the ground. The tissues thus changed weaken, lose their firmness and supporting power, and the seedling falls prostrate on the soil. The disease is wide spread and sometimes very common. It occurs not only in gardens and fields but is a very frequent attendant upon the culture of seedling plants in the forcing house or bed. The trouble is favored by damp soil, comparatively high temperatures, and humid atmosphere.

The term "damping off" is therefore indicative of one of the attendant conditions of the soil inducing the disease. While this popular expression is thus far significant of the trouble it is by no means the exact statement of the case. The plants do not damp off because of the abundant damp or moisture in the soil. The dampness encourages the growth of minute parasitic plants, not visible to the unaided eye, which pierce the seedling, feed upon its substance and set up disintegration processes which result in the death and collapse of the affected parts. Soon after the plant falls the dissolution of the tissues near the surface of the ground has usually proceeded so far that communication by the ordinary physiological processes of life is cut off, and the plant then withers and dies. While damping off is due to the action of minute fungus parasites, it is by no means caused by one and the same

Frontispiece. This is from a photograph of an experiment to show the parasitic nature of the *Artotrogus debaryanus* (Hesse). Before planting the cucumber seed the pots were filled with soil which was thoroughly wetted and then steamed in the steam sterilizer for several hours on three successive days in order to kill all the organisms. The seed was then planted and when just coming up some plant tissue with freshly developed stages of the fungus was placed by the seedlings in pots 5, 6, and 8, while pot 7 was left as a check. The result can be easily seen in the photograph, the check plants remaining unharmed while all the plants in 6 are killed and only one remains healthy in each of 5 and 8.

species. Different species of fungi may under some conditions produce nearly or quite identical phenomena in the progress and culmination of the disease. Some species develop phenomena allied to genuine cases of damping off, and the final result of which is practically the same, the decay of the stem near the surface of the ground and the collapse of the seedling.

Some variations in the external appearance furnish diagnostic characters correlated with the presence of certain species of the parasite, but it is doubtful if in any case the specific cause should be confidently asserted without recourse to microscopic examination, sometimes to be preceded by special treatment. In discussing the several species of fungi which have been found to contribute a share in the production of the disease it will be convenient to take up first the species to which the trouble is generally attributed, and then to follow with others which play a more or less important part in the development of similar or nearly identical troubles.

THE POTTING BED FUNGUS.

*Artotrogus debaryanus*¹ (Hesse).

This fungus is responsible for a large part of the damping off of young seedlings. It is very widely distributed, being very common in the soil of gardens and also in the forcing house. It is common also in many fields, but it probably is more abundant in soil where numbers of plants are grown from the seed in a more or less crowded condition, especially those plants which are known to be predisposed to its attacks. It has however been found in virgin soil taken freshly from the woods into the forcing house.²

It is thus a very common and unwelcome bed-fellow and pot-companion of many seedling plants which are more or less crowded

¹ *Pythium debaryanum* Hesse. The name *Pythium* was used in 1823 as a generic name for two species (*Mucor spinosus* Schrank, and *M. imperceptibilis* Schrank, Denkschr. d. k. acad. d. wiss. z. Munschen, 1813, 14) by Nees von Esenbeck Nova acta acad. Leop. XI, 2,515, which belong to another genus (*Achlya*, see Fischer, Rabenhorst's Krypt. Flora. IV, 332). *Artotrogus* (Montagne, Sylloge, 304, 1845) was the next name which was used for a member of this group and must consequently take the place of *Pythium* Pringsheim, Jahrb. wiss. Bot. II, 303, 1860.

² Humphrey, 8th Ann. Rept. Mass. St. Agr. Exp. Station, 221, 1860.

in the seed bed or forcing pots of our gardens and hot houses, especially if undue moisture is present in the soil. In the gardens it is frequently impossible to control the amount of moisture in the soil, and in the forcing house where often the light is defective, the air is not fresh or it is supercharged with moisture, it is often nearly or quite impossible by the ordinary methods to preserve that equilibrium of environment which will permit the growth of the seedling and at the same time check the growth of its inimical guest.

All experienced gardeners are probably familiar with the appearance of the diseased seedling when affected with the damping off fungus. At this day when the germ theory of disease, both animal and plant, has so completely poisoned the minds of all classes of people there is little difficulty in successfully advocating what is now an established fact, that the damping off fungus is a parasite in the seedlings and invades the tissue of the latter for the purpose of obtaining its food. It is fortunate therefore that especial attention can be given to setting forth the facts in the structure and development, and other peculiarities of the parasite, which are quite important to know in order to properly treat it, and also because it can then be distinguished from others either near or remotely related, some of which induce diseases in the early life of certain ferns or fern-like plants and cannot disease seedlings.

The first striking peculiarity in a bed or pot of seedlings affected with the disease which attracts our attention is the prostrate condition of a few plants while others are upright and apparently healthy. The prostrate plants are found to be shrunken at or near the crown, i. e. near the root or the surface of the ground. Frequently when our attention is thus first called to the disease the collapsed tissue of some of the prostrate plants is so far disintegrated as to be in a soft and rotted condition, so that on pulling at the plant it breaks easily at this point. Farther investigation will show that usually the entire root system is by this time decayed, while the greater part of the stem above ground and the young leaves are still green and possibly quite fresh, or flabby, or more or less wilted.

The conditions of the aerial portions of the plant at this early stage of its fall are largely dependent upon the moisture content of the atmosphere. If the moisture be quite dry the seedling will be quite flabby before it falls and will soon wilt thereafter, but if the moisture content is large the tissue will remain quite firm for a time unless the soil upon which it is lying is so saturated with moisture as to encourage the rapid growth of the fungus in the prostrate portion of the plant. When this is the case the entire plant soon becomes a putrid mass and the tissues often take on a dark color.

After attention has been called to the trouble by the preliminary collapse of a few plants, if others are carefully noted some will probably present a paler green color than the perfectly healthy ones, especially near the surface of the ground. If such plants are carefully examined they will probably show the presence of the fungus in the tissues of the root and lower part of the stem, for the fungus requires several hours after entering the tissues to produce such changes which would be visible to the unaided eye.

Mycelium. If from one of these prostrate plants a portion of the collapsed part of the stem is teased apart on a glass slip, such as is used in microscopic work, in a little water and then examined under the microscope the vegetative phase of the parasite will probably be apparent. It exists as slender, colorless, thread-like irregular tubes, which appear to be more or less tangled in the tissues of the seedling. These tubes are the *hyphae*, as they are called, of the fungus, and collectively make up the *mycelium*. The hyphae are branched in quite a profuse manner, the successive branches usually forming somewhat more slender hyphae than the parent ones, so that the main hypha is frequently larger than the branches.

The hyphae course between and through the cells. Where a hypha passes through a cell wall it is very much constricted or very much more slender than it is in the cell lumen of the seedling or between the cells. The hypha in boring its way through these walls excretes a ferment, it is supposed, which dissolves the cellulose of the walls at the point of contact. A quite minute opening in the wall is sufficient for the growing end of the hypha to squeeze its way through and maintain communication with the

older portion, and has the advantage of requiring a much less expenditure of energy than if the opening were made of the same size as the hypha. After passing through the cell wall the hypha enlarges to the normal size.

While the mycelium is comparatively young the inner portion of the hypha is continuous, i. e., there are no cross walls partitioning the tubes into sections. This is a characteristic possessed by a very large group of fungi to which the *Artotrogus* belongs, known as the *Phycomycetes*. The protoplasm within the hypha is finely granular when the mycelium is young, but in the larger threads as they become older the granules become coarser, their contents are not so homogeneous, and the granules tend to collect into groups or very irregular masses, somewhat resembling the protoplasm in some mucors.

In a crowded seed bed after a few plants have fallen, unless the disease is checked, it will spread from these affected ones as centers to others near them and thus from the one or several starting points the plants will fall until nearly or quite all of them have been killed. Where the soil and atmosphere is quite damp and the temperature conditions so high as to favor rapid growth of the fungus it will grow out from the diseased part of the stem into or on the surface of the soil for a few millimeters in extent as a very delicate cottony mass or velvety pile. Where the adjacent plants are not too far distant the superficial threads may thus reach them and communicate the disease to them. In other cases minute motile reproductive bodies called *zoospores*, or *swarm spores* (perhaps more properly *zoogonidia*) are developed in a manner to be described later. These swim in the soil water to the more distant seedlings and thus spread the disease.

Sometimes there will be seen quite a profuse growth of a mycelium, which on the surface of the soil may spread several centimeters in extent. Usually this profuse growth is that of another fungus, a *Rhizopus*, or *Mucor*, or in other cases a different "damping off" fungus to be described in a later paragraph.

If the tissues examined as described above from a seedling which has not remained long after falling over perhaps the condition of the mycelium described will be the only phase of the plant (for the fungus is a plant) at that time present. If it has

been dead for sometime, however, there will probably be seen here and there on the hyphae a number of rounded or spherical bodies, three to five times the diameter of threads of the mycelium with which they are connected. These are reproductive organs of the fungus and will soon be described.

The characters of the mycelium alone are not in all cases sufficient for the correct determination of the plant. Let then this preparation on the glass slip lie free in an abundance of water, and place the slip in a small moist chamber sufficiently protected so that the air in the chamber will not become dry by evaporation at the point of contact of the two vessels. This can be avoided by placing a sheet of wet filter paper between the cover and the edges of the bottom vessel. A Petrie dish, such as is used in bacteriological work, is excellent for the purpose. Some wet filter paper should also be placed in the bottom and on this the support for the glass slip can be placed. For hasty examination the material can be teased out directly in the bottom vessel of the Petrie dish in a little water, and then this can be placed on the stage of the microscope whenever it is desired to examine it.

In twelve to twenty-four hours if the preparation is again examined many threads of the fungus will be seen to have grown out from the tissue and spread on all sides for a distance of one to two millimeters in the surrounding water, now presenting the characters noted above in a clear manner, except there are no constrictions of the hyphae corresponding to those where they pass through the cell walls of the host. The branching is in an alternate or irregularly monopodial fashion. There will also be seen numbers of the rounded bodies noted above on the mycelium, both within the tissue and on the mycelium which is growing free in the water around its margin.

Sexual organs. Oogonia. The larger number of these rounded bodies in the case of this species will probably be what are termed oogonia. These are developed in several relations to the hyphae which bear them. They may be terminal, i. e. on the ends of the hyphae which bear them, or on the ends of quite short branches, or intercalary, i. e. when they appear as swellings of the hyphae here and there without any reference to the end.

A terminal oogonium begins as a slight swelling of the rounded

end of a hypha or short branch, which continues until the spherical body is about 18μ – 25μ in diameter. During its growth in size the protoplasm which fills the interior is supplied by the supporting hypha or oogoniophore, without, however, emptying any portion of the latter structure. When the oogonium has reached its full size, a septum, or partition wall, is formed cutting off its protoplasm from that of the stalk or oogoniophore. At this time the wall of the oogonium is thin and the protoplasm finely granular, though distinctly so, and completely fills the interior of the oogonium. The wall now increases somewhat in thickness, but remains colorless.

The egg cell of the oogonium is now soon differentiated, and in most cases, except where parthenogenesis takes place, is probably influenced by the development of the antheridium. The finely granular protoplasm of the oogonium becomes coarser and is gradually collected into numerous small irregularly rounded masses. At the same time all of the coarsely granular protoplasm contracts from the wall of the oogonium and moves toward the center forming there a rounded central mass somewhat less in diameter than that of the oogonium, being 14μ – 18μ in diameter. This central sphere of coarsely granular protoplasm is termed the oosphere, or egg cell, and is really an unfertilized egg, the receptive cell of the oogonium. Between this egg cell and the wall of the oogonium is a space filled with a nearly clear, but finely granular and homogeneous fluid called the periplasm. At this stage there is no wall surrounding the egg cell and it is ready to be fertilized.

Antheridia.—The sole purpose of the antheridia is to supply the fertilizing element for the egg cell, and the antheridium is sometimes termed the supplying gamete, while the oogonium is termed the receptive gamete. The antheridia are of two kinds, stalk antheridia and branch antheridia. A stalk antheridium is formed from a section of the oogoniophore by the formation of a partition wall in the hypha cutting off an elongated cell one end of which is thus in contact with the wall of the oogonium, and its contents are only separated from those of the oogonium by the wall of the latter. This is the simplest of the two forms of the antheridia.

A branch antheridium is developed as a lateral branch of the oogoniophore, arising usually quite near the oogonium, but sometimes more or less remote from it, rarely on a separate hypha. The branch grows towards the oogonium and its rounded end comes in contact with the oogonium wall and becomes fixed at the point of contact. A septum is now formed in the branch cutting off an elongated cell varying from 15μ – 40μ . This cell, one end of which is in contact with the oogonium wall, is the antheridium, and the proximal portion of the branch is the antheridiophore. More than one antheridium may be formed in connection with a single oogonium, frequently two and sometimes three. Both may be branch antheridia, or one may be a branch antheridium and the other a stalk antheridium, and other combinations may take place where more than two antheridia are present. There does not seem to be any rule in the number of antheridia which take part in the fertilization of the egg cell. Where several are in contact one or more may take part in the act of fertilization.

When the antheridial cell is formed its farther development is the same whether it be a branch antheridium or a stalk antheridium. The cell which is cylindrical or nearly so in form begins to swell and this continues until it is two to three times the original diameter, the greatest diameter being near the end which is in contact with the wall of the oogonium. At the same time it also becomes quite strongly curved and more or less twisted. In case the oogonium is a terminal one and possesses both a stalk antheridium, and branch antheridium, the stalk antheridium may curve so strongly to one side as to make it difficult to determine later which is really the stalk antheridium.

While these changes are taking place in the antheridium the granular protoplasm of the oogonium is moving toward the center to form the egg cell as described above, and now the end of the antheridium in contact with the wall of the oogonium, puts out a slender tube which pierces the oogonium wall, extends across the space occupied by the periplasm and touches the egg cell at the nearest point. This tube is known as the fertilization tube. At this point on the egg cell there is a small clear space called the receptive spot.

Nearly all of the protoplasm in the antheridium except a very

thin layer next the wall becomes coarsely granular, arranged in strings and is finally collected in the middle line of the antheridium. This is known as the gonoplasm, and soon passes through the fertilization tube and is emptied into the egg cell at the receptive spot, where it disappears in the substance of the egg cell and completes the act of fertilization.

While the passage of the gonoplasm is going on it can be seen that a thin wall is forming around the egg cell over the surface except at the point where the fertilization tube is located. When the gonoplasm has passed through, the wall becomes complete at that point, and the entire wall then thickens somewhat and soon becomes brown in color. The fertilized egg cell now becomes the egg, or oospore.

These phenomena in the development of the oogonia and antheridia and in the fertilization of the egg cell can be quite easily followed by teasing out a small section of the diseased plant tissue in water on a cover glass and arranging this for a cell culture in what is known as a van Tiegham cell. This can be placed on the stage of the microscope from time to time and the development traced. From such a culture made from a diseased young melon seedling the following record was made. The diseased tissue was teased out in water on a glass slip Monday, Jan. 28, and placed in a moist chamber. The following day, Jan. 29, a profuse growth of mycelium, oogonia and antheridia had taken place, the mycelium extending for 2mm to 3mm out from the diseased tissue. Jan. 30 a small portion of this tissue was farther teased out and mounted in fresh water in a cell culture. Jan. 31 farther growth had appeared and new oogonia and antheridia were developed. This continued for several days in the same culture.

On Feb. 1 at 12:30 P. M. as shown in fig. 1, the egg cell in the oogonium has formed and the antheridium curved over on one side is full size but the fertilization tube has not yet formed nor has the gonoplasm differentiated, the granular protoplasm being arranged in a network of threads. At 3:15 P. M. of the same day as shown in fig. 2 the fertilization tube is complete, the gonoplasm has formed and is about to pass through the tube, while a very thin wall is forming around the egg cell except at the receptive spot. At 9 P. M., fig. 3, the gonoplasm has passed through and the wall

of the oospore is complete. Fig. 4 represents an intercalary oogonium which was observed in the stage figured, at 12:30 P. M., Feb. 1. Two antheridia are here in contact with the oogonium *s. a.* a stalk antheridium and *b. a.* a branch antheridium. In both cases the fertilization tube is complete, and the gonoplasm has separated preparatory to passing through. The curving of the stalk antheridium has turned the main thread to one side, the branch antheridium arising quite closely by the side of the oogonium has curved inward to the wall of this organ. At 3:30 P. M., fig. 5, the gonoplasm has passed through the fertilization tube from both antheridia and a thin wall has formed around the now fertilized egg. Fig. 6 at 12 P. M., showed a terminal oogonium with two antheridia, one a stalk antheridium and one a branch antheridium, it being difficult in this case to say which is the stalk and which is the branch. An accident happened to this specimen and it was not seen again. Fig. 7 represents two terminal oogonia each with a stalk antheridium, first observed at 9 P. M., Feb. 1. At this time in the case of oogonium *a*, the egg cell is formed, and the gonoplasm in the antheridium has separated, while in oogonium *b*, the egg cell has not yet formed. From the fact that the stalk antheridium was on the under side of oogonium *b*, when it was first observed, the stage of its development could not be seen. At 2 P. M., on Feb. 2, however, fertilization was completed in both as shown in fig. 8. Fig. 9 represents an oogonium with a fertilized egg and two antheridia in contact with its wall; one, *a*, a stalk antheridium whose gonoplasm took part in the act of fertilization, and one, *b*, a branch antheridium from a different hypha from that on which the oogonium is borne. From the latter the gonoplasm was not used.

These oospores or fertilized eggs mark a very important phase in the life history of the fungus. They will eventually germinate and produce the mycelium again, which under favorable conditions will start the disease anew. But the remarkable thing about the oospores is that they cannot germinate immediately, except in rare instances, but must undergo a long period of rest, and hence are sometimes termed resting spores. In this condition they are capable of resisting degrees of cold and dryness which would prove fatal to the vegetative portion of the fungus. This accounts partly

for the appearance of the disease after long periods of drought and after the inclement weather of the winter season in some sections.

Not only does the thicker wall of the oospore offer greater protection against an unfavorable environment, but the protoplasm undergoes a marked change before it finally enters upon this enforced period of rest. This change is practically a metamorphosis, the complete nature of which we do not understand. Among other changes there is probably a change in the molecular or physical structure of the protoplasm by which a large amount of a fatty substance is separated and forms a very large globule and sometimes other smaller ones which occupy a large part of the space of the oospore. The protoplasm thus becomes transformed into a state highly resistant to outside conditions and incapable of growth for a long period, even though the environment may be most favorable for growth. The period of rest lasts for several, four to five, months. They will resist freezing for weeks, followed by drying, without injury.

Propagative organs. Organs of another kind than oogonia and antheridia are developed on the mycelium. The function of these is chiefly for the immediate and rapid propagation of the numbers of the parasite. The organs are, like the oogonia, either terminal or intercalary swellings of the hyphae, and at first do not differ materially from them before the differentiation of the egg cell and antheridium. These organs are exactly alike in form but differ in the discharge of their functions and are termed respectively, conidia, resting conidia, and zoosporangia.

Conidia. The conidia measure about the same as the oogonia and when fresh water is added to them they will germinate immediately after maturity, which is attained upon reaching their full size.

Resting conidia. These are conidia which do not germinate immediately and acquire a somewhat thicker wall than the conidia. They pass through a period of rest before germinating. They are identical in form and size with the conidia. They are capable of growing after being frozen, and after drying, and serve in this way much the same function that the oospores do in that they tide the fungus over quite long periods which are unfavorable for the growth of the plant.

In germination the conidium thrusts out, by an extension of

its wall, at one or more points, a slender tube which elongates into a hypha exactly like those of the former mycelium. This enters a young seedling when favorably situated, and starts the disease again.

The conidia and zoospores are rarely developed so abundantly in this species as are the oogonia. In my cultures during Jan. and Feb. 1894-5 the oogonia were far more abundant and no zoosporangia were observed. DeBary says that sometimes one may search for weeks and even months and not find zoosporangia. I have therefore not had as yet an opportunity of studying the formation of the zoospores from the zoosporangia and cannot say whether or not they agree with those of *Arlotrogus intermedius* (deBary), which will be described in the next paragraph. The following account is therefore abbreviated from published descriptions.³ The zoosporangia are usually not to be differentiated from the conidia until the time for the development of the zoospores. They are either terminal or intercalary, and sometimes so much of the protoplasm migrates into them during development from the supporting hypha that this is emptied for a short distance near the point where the wall separates the zoosporangium from the contents of the hypha. They usually remain attached to the supporting hypha and at the time of maturity, if placed in fresh water containing oxygen, a short protuberance is developed on one side at nearly right angles to the supporting hypha, which grows to a very short tube of a varying length but always shorter than the diameter of the zoosporangium. Into this tube the protoplasm migrates and causes the end of the short tube to swell out into a rounded vesicle of about the same diameter as that of the zoosporangium, with a thin enclosing membrane. The protoplasm now breaks up into a number of kidney shaped masses, with two lateral cilia according to most authors, although Hesse⁴ who first described the process in this species says that the zoospores are oval and uniciliate. These swarm about in the water for a few minutes, come to rest, round off and germinate in the ordinary way for conidia by sending out a slender germ tube

³ DeBary, Zur Kennt. d. Peronosporreen, Bot. Zeit. 39, 521, 1881, Beitr. z. Morph. u. Phys. d. Pilze, IV, 1881.

Schroeter, Pilze, in Engler u. Prantl, Naturl. Pflanzenfam. 1, 1 104.

⁴ Hesse, Pythium debaryanum, ein entophytischer schmarotzer, Halle, 1874.

which when favorably situated will start the disease in fresh plants. It is probably by the development of these in wet soil during rain or at the time of watering the pots or soil in seed beds that the disease is spread so rapidly.

The fungus is however capable of developing as a saprophyte on dead or partially decayed organic matter in the soil so that with one watering it may become well seated in nearly all parts of the bed. To show that it is also a saprophyte it is a very easy matter to start it in the laboratory on the leaves or stems of seedlings which have been previously killed by boiling.

This damping off fungus was first described by Hesse in 1874 (l. c.) and named by him *Pythium debaryanum*. It was shown by him to be a parasite of seedlings, such as *Camelina sativa*, *Trifolium repens*, *Spergula arvensis*, *Panicum miliaceum* and *Zea mays*, while seedlings of *Solanum tuberosum*, *Linum usitatissimum*, *Papaver somniferum*, *Brassica napus*, *Ornithopus sativus*, *Onobrychis*, *Pisum*, *Hordeum vulgare*, *Triticum vulgare* and *Avena sativa* were not attacked.

DeBary made a comprehensive study of the sexual stage.⁵ *Pythium equiseti* Sadebeck, is in his opinion the same species. *P. equiseti* was first described by Sadebeck⁶ in 1874 from prothallia of *Equisetum arvense*, and in farther studies⁷ it was shown that not only did it occur in potatoes affected with *Phytophthora infestans*⁸ but that healthy potatoes could be inoculated with it. *Pythium autumnale* Sadebeck which grew in young plants of *Equisetum palustre* and *E. limosum*, produces oospores which develop parthenogenetically. Fischer⁹ places this in *P. debaryanum*. A plant found in *Lepidium sativum*, and in *Beta* and *Sinapis* by Lohde,¹⁰ was described by him as *Lucidium pythioides* and from

⁵ Beitr. z. Morph. u. Phys. d. Pilze, IV. 1881.

⁶ Ueber einen der familie der Saprolegniaceen angehorigen Pilze in dem prothallien des Ackerschachtelhalmes. Sitzungsab. d. Bot. Ver. d. Prov. Brandenburg, 116-122, 1874.

⁷ Neue Untersuchungen über *Pythium equiseti*. Sitzungsab. d. Gesells. naturf. Freunde z. Berlin, V. 21, 1875.

⁸ Ueber Infectionen welche *Pythium*-Arten bei lebenden Pflanzen hervorbringen. Beibl. z. Tageb. d. 49 Vers. deutscher naturf. u. Aertze. 100, 1876.

⁹ Rabenhorst's Krypt. Flora. Pilze, IV, 404, 1892.

¹⁰ Ueber einige neue parasitische Pilze. Tagebl. d. 47 Vers. deutscher Naturf. u. Aertze, 203, 1874.

the description there is little doubt that it is the *Artotrogus debaryanus*. *L. circumdans* described by the same author in a fern prothallium¹¹ develops only in the margin of the same, producing short conidiophores and zoosporangia with 4-8 zoospores. Fischer¹² also includes this with *P. debaryanum* Hesse, as well as the *Saprolegnia schachtii*¹³ described by Frank in the thallus of the liverwort *Pellia epiphylla*. Zoospores were not seen and oogonia only rarely, the plant being usually sterile.

A number of these are probably rightly referred to *Artotrogus debaryanus* (Hesse). Unfortunately these plants cannot well be preserved for study in their several stages and in most of the cases probably no specimen of any stage has been preserved, so that it would be quite impossible at the present time at least to speak with any feeling of certainty on the proper disposition of these forms. There is need of a thorough and comprehensive study of the species of the genus, and considerable uncertainty will probably exist as to the proper disposition of some of the above species until they can again be found and critically studied.

The fungus has been several times reported in this country, and many notices of damping off have been made without, probably,

¹¹ Ueber einige neue parasitische Pilze. Tagebl. d. 47 Vers. deutscher Naturf. u. Aertze, 203, 1874.

¹² Rabenhorst's Krypt. Flora, Pilze, IV, 404, 1892. 4 Ibid.

¹³ Notes on the fungus causing damping off, etc. Trans. Mass. Hort. Soc. I. 1891.

Explanation of Plate I. *Artotrogus debaryanus* (Hesse).

Figs. 1, 2 and 3, different stages in fertilization; *a* antheridium, *oog.* oogonium, *e. c.* egg cell, *gon.* gonoplasm, *oosp.* oospore.

Figs. 4 and 5 intercalary oogonium with stalk antheridium (*s. a.*) and branch antheridium (*b. a.*), in 4 with gonoplasm separated from the periplasm, and in 5 fertilization complete.

Fig. 6 terminal oogonium with stalk and branch antheridium.

Figs. 7 and 8 different stages in development, and fertilization, of sexual organs; *b* in 7, oogonium before the formation of the egg cell.

Fig. 9 oogonium with stalk antheridium (*a*) which has fertilized the egg cell, and branch antheridium (*b*) from another hypha than that which bears the oogonium. In this branch antheridium the gonoplasm has separated, and the fertilization tube has formed, but fertilization took place from the stalk antheridium first and the wall of the oospore prevented the use of the gonoplasm from the branch antheridium.

All the figures drawn with aid of camera lucida and magnified 50 times more than the scale. Scale—1 millimeter.

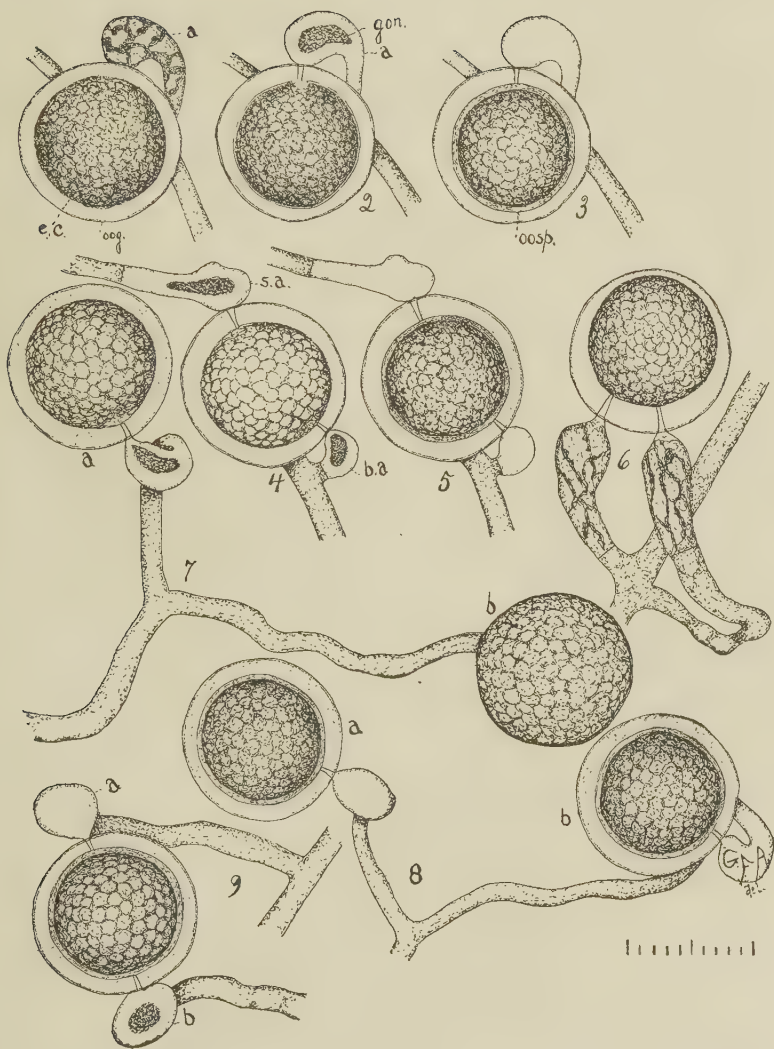


PLATE I.—*Artotrogus debaryanus* (Hesse).

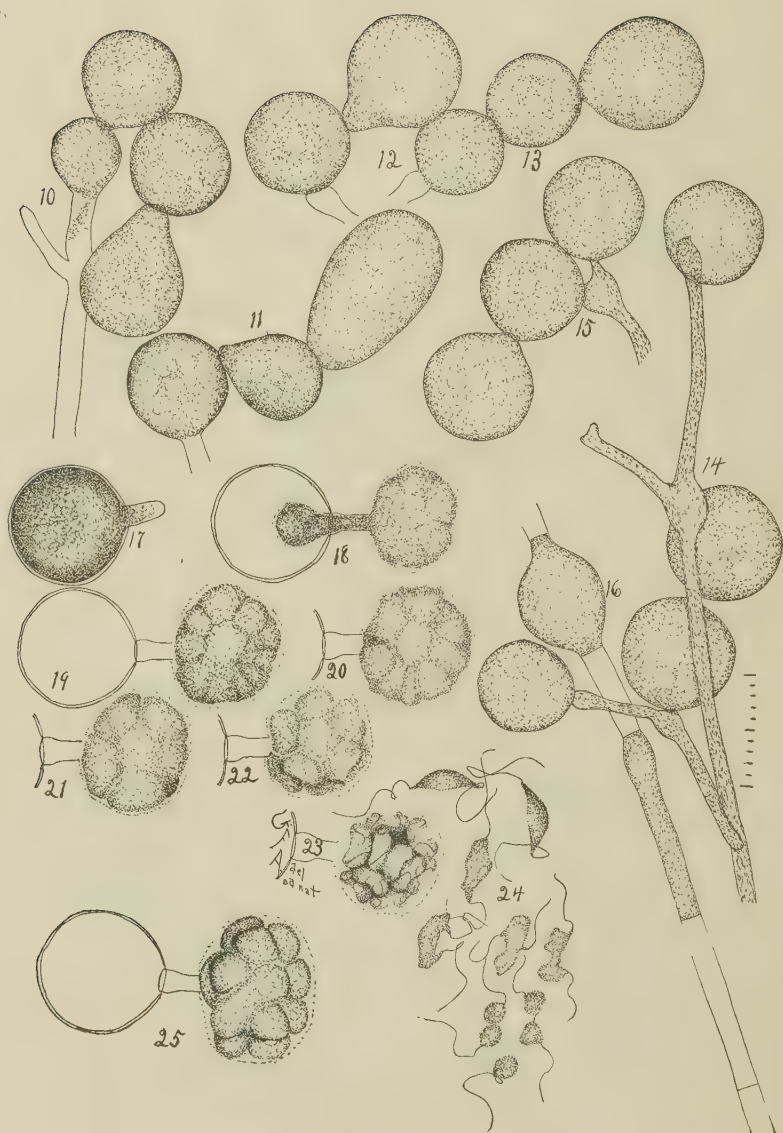


PLATE II.—*Artotrogus intermedius* (de Bary).

any serious attempt to determine the species. T. W. Galloway from a careful study determined it from seedlings of *Gilia*, *Viscaria*, *Lobelia*, etc., in the Botanic Garden of Harvard University. He did not however observe the zoospores. Humphey¹⁴ also carefully determined the species, but does not describe the zoospores.

DAMPING OF PROTHALLIA.

Artotrogus intermedius (deBary).

This species was first noticed in fern prothallia growing in the botanical conservatories of Cornell University in the month of February, 1894. The affected prothallia were quite soft, limp, and darker in color than the healthy ones. Some were placed in water on a glass slip and kept in a moist chamber. The following day the fungus had grown out of the prothallial tissue and had extended a considerable distance over the slip. The mycelium is at first non setate and contains granular protoplasm which is present in minute irregular masses, having in the larger threads much the appearance of the protoplasm in some mucors, and in some cases well marked and strong currents of the protoplasm have been observed, which resemble the movement of the protoplasm in these plants.

The threads branch monopodially, the extent of the branching depending, to a certain extent on the amount of the vegetive growth. The threads put out in the water from the prothallia may be quite long and possess primary and secondary branches before conidia are developed to any great extent. The conidia are developed at the ends of the main threads or their branches, the hypha swelling at the end into a rounded body several times the

¹⁴ 8th Ann. Rept. Mass. State Agr. Exp. Station, 220, 1890.

Explanation of Plate II. *Artotrogus intermedius* (deBary).

Figs. 10, 11, 12, 13, conidia developed in chains.

Figs. 14 and 15, conidia borne in a manner resembling the conidial fructification in *Phytophthora*.

Figs. 17-23, different stages in the development of the zoospores.

Fig. 24, free zoospores with a cilium at each pointed end, passing into amoeboid movement and becoming divided into oval unciliated zoospores.

Fig. 16, intercalary conidium.

All the figures from camera lucida drawings and magnified 50 times more than the scale. Scale 1 millimeter.

diameter of the thread itself. In other cases the thread may develop a conidium while it is still quite short and the growth of the thread in length practically cease. In other cases the conidia are developed at the ends of the primary or secondary branches as well as at the end of the main hypha. Where the conditions are not favorable for the rapid growth of the vegetative portion of the plant, sometimes the conidia are developed more profusely and rapidly so that they are many times produced in chains. Frequently these are in nearly straight chains, or they may form a curve, or again a short and close spiral so that they are held close to the point of origin in a small head.

The conidium may be spherical or broadly apiculate at the proximal end or more minutely apiculate at the distal end. Sometimes there is no enlargement of the fruiting thread at the point of origin of the conidium, but very frequently, and in a majority of cases which I have observed where they are grown in water, there is an oval enlargement of the hypha with a minute apical sterigma which bears the conidium. Where there is quite rapid growth of the fungus the hypha grows onward pushing the recently developed conidium to one side but not always freeing it, and soon bears another conidium in like manner. This continues so that several conidia may be borne at short intervals on the same branch, and the successive points of the origin of the conidia are not only marked by the attached conidia but by the oval enlargements on the branch. The appearance is thus in many cases very much like that of the conidiophores of *Phytophthora*, and deBary has called attention to the same fact. Many of the conidia become free.

Early in April of the same year cultures were again started on glass slips in water. A preparation was started Tuesday afternoon, April 10, at 3 P. M. At 6 P. M. considerable growth had taken place and several conidia were developed. At 9 P. M. another examination was made and quite a profuse growth was present and numerous conidia or zoosporangia.

At 9 A. M., Apr. 11, there were many free conidia and zoosporangia and the culture abounded in the form of fructification which so closely resembles *Phytophthora*. Fresh water was now added to the preparation, a cover glass placed upon it for the purpose of studying it with the high power of the microscope and for obtain-

ing camera lucida drawings. After making several sketches of desired objects one zoosporangium was discovered emitting the protoplasmic vesicle preparatory to the differentiation of the zoospores. When the eye first fell upon it the object was in the phase represented by Fig. 18. Soon the protoplasm had all passed through the short tube and was collected in a rounded vesicle at the end. There was a slight differentiation of the protoplasm at the time of the passage, but it was little marked. The differentiation became more and more marked showing that the mass was dividing into ten to twelve polygonal bodies. The surface of the forming zoospore next the wall of the vesicle, or the periphery, is the longer, and at the middle of the outer surface of the object there soon appears a depression which gives each a curved appearance. This form becomes more and more marked and now movement begins, which first appears as a kneading of the entire mass, and as they become more and more sharply differentiated each young zoospore produces an oscillatory movement with its center nearly stationary, the movement of course much restricted by the surrounding vesicle. As they assume more distinctly the curved appearance there is developed from each end of the zoospore a cilium by the lashing of which the movement becomes more violent and results soon in the release of the swimmers when they suddenly dart away.

The movement is now a complex one. The oscillatory movement is more marked with a tendency in many cases to produce figure of 8 cycles, which is combined with a jerky progressive movement in the direction of the longitudinal axis. Frequently when they come in contact with some object larger in size, they simulate to some extent the movements of a paramæcium along some object in the water.

The form of the mature zoospore is broadly fusoid, inequilateral with pointed ends which terminate in a long cilium. After five to ten minutes the movement of the swarm spores becomes slower and finally it nearly ceases and the body undergoes plastic movements resembling somewhat that of an amoeba as represented in Fig. 24. At first this amoeboid movement is irregular but after a few minutes it assumes a definite character which tends to cut the organism into two parts. This progresses until complete

fission results in the formation of two zoospores which are oval in form with the cilium attached directly at the smaller end.

This peculiarity in the development of the zoospores is one which has not heretofore been recorded except in a preliminary paper by the writer.¹⁵ The species was at that time studied along with the seedling fungus, *A. debaryanus* (Hesse), and as this is reported as occurring also on fern prothallia (*Todea africana*) the species now under discussion was then supposed to be the same, and to this species it was doubtfully referred. But the development of the conidia is very different from that described for any other species of this genus resembling that of *Phytophthora* as stated above.

It cannot therefore at the present time be said with certainty that the zoospore formation in *Artotrogus debaryanus* is the same as that found for *A. intermedius*, though what evidence we already have on the subject might be interpreted to support that view of the case.

Where the soil is kept very damp and the air of the house is quite humid the prothallia are apt to be overrun by certain algae which choke the prothallia, shut out the air and light, prevent their proper development and frequently cause them to be completely sterile. Many of the prothallia are thus killed, sometimes entire beds or pots of them. A very common alga which I have several times observed is a variety of *Hormiscia flaccida* (Kuetz.) Lagerh. Species of *Oscillatoria* are also frequently present and produce a like injury.

If the pots or vessels in which the prothallia are grown are rested on sphagnum a layer of which can be placed in the bottom of the wardian case, and after the young prothallia have started, all of the watering be applied through this, the prothallia will do much better than if surface watering is practiced and far better than where the pots are rested in a vessel partly full of water. The air of the wardian case or of the house should not be kept too damp.

NOTE ON THE GENUS ARTOTROGUS.

Hesse who first described *Artotrogus debaryanus*¹⁶ (*Pythium de-*

¹⁵ Preliminary note on the swarm spores of *Pythium* and *Ceratiomyxa*, *Bot. Gaz.* XIX, 375, 1894.

¹⁶ *Pythium debaryanum*, etc. Halle, 1874.

baryanum Hesse) says as stated above that the zoospores are oval and provided with one cilium. *Pythium equiseti*¹⁷ Sadebeck which is generally considered to be the same plant, possesses two lateral cilia according to the descriptions, and deBary only says that the zoospore formation takes place in the oft described way.¹⁸ In *Artotrogus proliferus*¹⁹ (deBary), the author was unable to determine whether the zoospores were uniciliate or biciliate. In the vesicle they are figured as reniform, but the ultimate zoospores are described as oval, one end being narrower than the other. Double zoospores were also described which possess two light spots instead of one. These ultimately divided, but before division according to the author, the double zoospore was like that of an organism controlled by two opposing wills. This was not the case with the biciliated zoospores observed by myself in *Artotrogus intermedius*, until amoeboid movement was beginning after a period of swarming, and when fission is about to take place. Possibly deBary observed the "double" zoospores just at that time.

(In *Artotrogus pythiodes*²⁰ (R. et C.) the zoospores are described and figured as biciliate one cilium attached at each pointed end of the zoospore exactly as I have found in the case of *A. intermedius*. But in *A. pythiodes* the authors say that the zoospores absorb the two cilia, round off and germinate, i. e. they do not divide, if the observations are clear on this point. This species was found on leaves of *Wolffia mitchellii*.

Other species of the genus are as follows. *A. hydnosporus*²¹ Mont. in potatoes and in dead seedling plants: ²² *A. ferax* (deBary) in dead insects and in dead seedlings in water. *A. megalacanthus*²³ deBary in dead seedlings and parasitic in prothallia of *Todea*

¹⁷ Untersuchungen über *Pythium equiseti*, Cohn's Beitr. z. Biol. d. Pfl. III. 117.

¹⁸ Zur Kenntniss der Peronosporéen, Bot. Zeit. XXXIX., 524, 1881.

¹⁹ *Pythium proliferum* deBary, Pringsh. Jahrb. f. wiss. Bot., II, 182, 1860.

²⁰ Roze et Cornu, sur deux nouveaux types generiques pour les Familles des Saprolegnees et des Peronosporées, Ann. d. sci. nat. Bot. ser. 5, II. 72, 1869.

²¹ Montagne, sylloge, etc., p. 304, 1845.

²² Bot. Zeit. XXXIX., 562, 1881.

²³ Beitr. z. Morph. u. Phys. d. Pilze. IV., 19, 1881; Bot. Zeit. XXXIX., 578, 1881.

africana. *A. proliferus*²⁴ (deBary) saprophytic on dead seedlings and insects in water; *A. vexans*²⁵ (deBary) in dead seedlings and in diseased potatoes; *A. anguillulae-aceti*²⁶ (Sadebeck), parasitic in *Anguillula aceti*; *A. sadebeckionus* (Wittmack) producing epidemics of diseases in lupines and peas. Several other species have been imperfectly described.

A POTTING BED FUNGUS NEW TO AMERICA.

Completoaria Complens Lohde.

This is an organism which is parasitic upon fern prothallia grown in forcing houses. It has been known in Europe for several years but was first found in this country during the winter of 1893-4, in the botanical conservatories of Cornell University, while studying the rotting of prothallia induced by *Artotrogus intermedius* (deBary), described in a former paragraph of this paper. Ultimately the prothallia decay but the first signs of disease when caused by this parasite alone is the appearance of a yellowish or yellowish brown color imparted by the prothallia as they lie on the soil of the pot or bed. The prothallia are so small that usually the color appears to reside in the entire prothallium when seen by the unaided eye. When examined by the aid of a microscope, however, unless the prothallium is in the last stages of the disease, the decay will be seen to be confined to "spots."

These spots vary in color from a yellowish green to yellowish brown, deep brown and finally blackish, dependent on the phase of the injury to the cell and its contents. At first the injury is confined to single cells either near together or far isolated, on the margin of the prothallium or at any point over its surface.

When the trouble is well advanced and there are numerous centers of the disease, as frequently happens, the prothallium will present a checkered or mosaic appearance, the different pieces of the mosaic being colored with the various shades of color detailed above. It also presents at this time quite a ragged appearance because many of the cells are dead and the disintegration of their contents makes holes in the plant and rifts in its edges. A short

²⁴ Pringsh. Jahrb. f. wiss. Bot. II., 182, 1860.

²⁵ Jour. Bot. V., 119, 1876.

²⁶ Bot. Centralbl. XXXIX., 318, 1887.

note on the occurrence of this fungus in the United States was published by the writer in the *Botanical Gazette* for November, 1894. It is a very interesting fungus from its very simple structure, its peculiar form, mode of development, and as a plant parasite, from its being a member of the *Entomophthoreae*, which are almost entirely parasites of insects.

The vegetative body of the fungus is a more or less compact, grape like, or botryose cluster of oval or curved hyphal branches originating from a common center, and presenting on the surface a series of convolutions formed by the external hyphal branches lying close together over the surface. This vegetative body lies within a single cell of the prothallium, sometimes completely filling even quite large cells, while at other times the body may be smaller especially in smaller cells of the prothallium, where it sometimes consists of only a few hyphal branches closely curved upon their parent cells. These hyphal branches vary from 7μ to 15μ in diameter or may even be of a greater diameter, and are one and one-half to two times longer. When the plant body in a single cell becomes mature it may spread to the surrounding cells by certain of the external hyphal branches putting out a slender germ tube which pierces the adjacent intervening wall. This is done by the tube of the hypha excreting a substance which dissolves the cellulose of the wall making a small minute pore and at the same time turning the adjacent portions of the wall brown in color. The wall of the slender thread which squeezes its way through this opening is also colored brown, and this color is frequently extended to the slender portion of the thread or tube, in which the protoplasm passes or migrates to the center of the cell as shown in figure 44.

When it has reached the center of the cell lumen the free end enlarges and forms a rotund body which finally becomes oval. At this time it is about 15μ to 25μ in diameter, with quite coarsely granular protoplasm and with one or more large vacuoles. By this time also all of the protoplasm from the original cell has moved into this oval body in the center of the cell, leaving behind only the wall of the slender tube by which it gained entrance and which is still connected with the wall of the living organism. This old wall as well as the wall of the prothallial cell where the organism entered becomes brown in color soon after the proto-

plasm has passed through into the center of the cell of the host. From the free and smaller end of this oval cell a short protuberance grows curving to one side usually rather close to the side of the parent cell. Sometimes this branches quite soon in a dichotomous manner and the two short cells curve in opposite directions. If dichotomy does not occur at the beginning of the protuberance another branch arises soon from the original cell or from the branch. These protuberances become enlarged at a very short distance from their origin forming oval cells. These in like manner produce short branches, and the process continues until a botryose or convoluted mass of cells is developed which eventually fills the cell of the prothallium, and the elements of the botryoid body become angular from mutual pressure. The wall now becomes brown in color and the glomerule appears to be mature.

In this condition if these hyphal masses are teased out from the cell of the prothallium and kept on a glass slip in a small amount of moisture germination soon takes place. Hyphal masses so teased out from the prothallium and placed under the above conditions at 5 P. M. on Feb. 22, 1894, and kept at the ordinary room temperature during the night, the temperature falling somewhat below that of the day (the temperature was 70° to 80° Fahr., up to midnight and fell 30 toward morning and rose to 66 at 9 A. M.). At 9 A. M. Feb. 23d, the preparations were examined and the mature hyphal masses were germinating. In some cases the germ tubes were 500μ to 700μ long and all the protoplasm had moved out in the distal half of the tube (fig. 42). In germination under such circumstances a protuberance arises from one of the individual cells of the glomerule and extends soon into a tube the diameter of which is about 10μ . As the tube extends in length the protoplasm gradually disappears from the parent cell and passes into the tube. As the tube continues to elongate the protoplasm continues in the distal portion and the older portion of the tube becomes empty, nothing remaining but the wall. There appears to be a wall at the junction of the tube with the parent cell, if so it is formed after the protoplasm has passed into the tube. When the tube has become considerably elongated so that there is an empty portion from 200μ to 500μ in length there appear what seem to be transverse septa, or it may be the remains of a portion of the protoplasm situated in a thin transverse sheet in the tube. These

occur so regularly and at about 30μ to 40μ distant that the resemblance to septa is very striking if they are not really septa. If they are septa they are formed only after the protoplasm has passed these points. It may be that the growth of the tube was arrested for a certain length of time and the walls were formed while it was in this quiescent condition, or the growth of the tube may be naturally periodic. The protoplasm is coarsely granular, presenting here and there rather faint vacuoles, but there are so far as examined, no septa separating the protoplasm into distinct portions. The course of the tube is slightly sinuous, and also in an ascending position as the glomerule lay on the glass slip. Perhaps this was for the purpose of emerging from the water. After an examination the cultures were returned to the moist chamber.

While the fungus is progressing through a prothallium when one of these spore balls becomes mature, some of the cells lying adjacent to healthy cells of the prothallium germinate and grow directly into the new cell host. In doing so the germ tube is very much smaller since less energy is expended in making the perforation through the wall. After emerging from the wall in the new host cell the tube does not enlarge to the size of the tube when germination takes place in water on the glass slip, but remains about the same size as that of the perforation in the wall, until it reaches the center of the cell lumen where it enlarges into a rotund body as described above. Here it soon grows into the botryoid hyphal mass again. Other cells may germinate and course for a considerable distance over the surface of the prothallium and enter new host cells quite distant from the hyphal mass, but this has not been observed. In some cases more than one cell lying quite close to a new host cell will germinate and grow into the same. From the observations thus far made I should judge this to be quite common but not general.

The first ovoid portion of the mycelium in the center of the cell of the host is considerably larger than the curved branch which develops at its apex and frequently larger than any which follow. The more slender form of these branches and the close apposition of the branches to the primary enlarged ovoid portion suggests a striking resemblance to an oogonium and antheridium. Thus far I have not seen any conclusive evidence that these organs are

present. However, frequently the conditions are favorable for the development of another form than the purely vegetative portion of the plant, and either simple resting spores are developed, or if sexual organs are present, then oospores. The number of resting spores varies from one to ten or even twenty in large prothallial cells where the botryoid fungus is well developed. The resting spores occupy the central portion of the mass and are surrounded by the smaller and terminal cells of the plant which now are empty. The resting spores are rounded, sometimes oval, in form and when mature are bounded by a very thick wall consisting of three coats which are smooth, but sometimes appear roughened by the closely cohering cell walls of the collapsed surrounding terminal portions of the botryose mycelium. The portions which become resting cells are always the larger and central portions. They are much larger at the time of the formation of the resting spores than when the fungus is in the vegetative stage, and since at first there appear to be no cell walls intervening it would seem that their increase in size came chiefly from the outer and smaller cells giving up to them their protoplasmic contents rather than that the additional nutriment came from the cell of the host which by this time is nearly exhausted. However, this point was not determined. The wall of the young resting spore is at first very thin and the protoplasm finely granular. The mature resting

Explanation of Plate III. *Completozia complens* Lohde.

Figs. 26-30 different plants with mature resting spores showing the variation in number developed in a single plant; the resting spores surrounded by the empty peripheral cells of the plant, which may have developed conidia, or some of them entered adjacent cells of the prothallium, or possibly some of them fed the developing resting spores.

Figs. 31-32, younger stages in the development of the resting spores.

Fig. 34, plant developing resting spores at the center and a conidium from one of the peripheral cells.

Fig. 35 conidium germinating; 36, 37 and 39 germinating conidia with the germinal vesicles or proembryos developed from each one.

Fig. 40 germinal vesicle or proembryo developing the minute entrance tube which pierces the wall of the cell of the prothallium, 38 showing the entrance tube complete and the protoplasm having migrated to the center of the cell where the rotund body is formed, 41 branching of young plant in cell of host.

Drawn with aid of camera lucida and magnified 30 times more than the scale. Scale, 1 millimeter.



PLATE III.—*Completoria complens* Lohde.

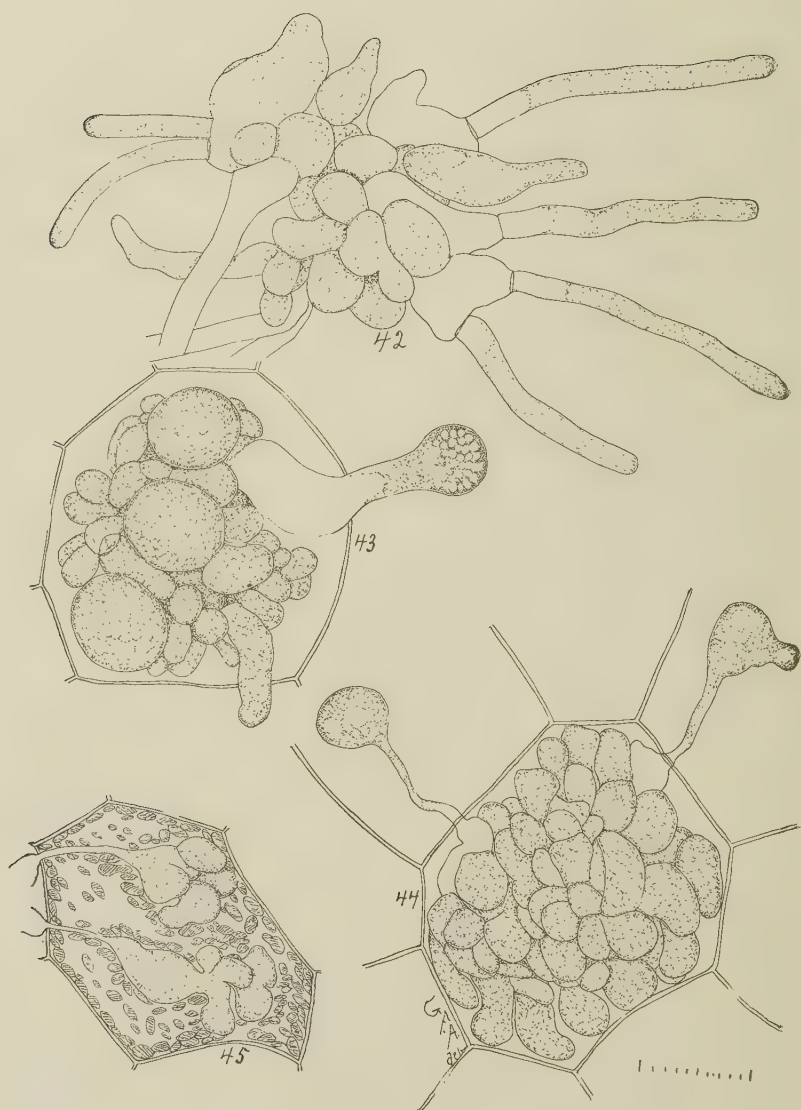


PLATE IV.—*Completoria complens* Lohde.

spore presents a very coarsely granular protoplasm the granules rounded in form and closely packed together.

Propagation also takes place by the production of non-motile Conidia from monosporous sporangia.

The conidia are oval or broadly obovate, colorless cells, with a thin wall and measure from 15μ to 25μ in diameter. In germinating, unless they are lying entirely immersed in water or in an abundance of a water which may be on the surface of the prothallium or on the soil, they do not form a mycelial tube directly. A very short tube is formed and into this the protoplasm migrates and causes the end of the short tube to swell out into an oval or oblong vesicle or the vesicle may be separated from the conidium by a constriction. This phase reminds one of the formation of the zoospore vesicle in the species of *Artotrogus*. But the formation of this tube and of the vesicle does not take place so rapidly as in *Artotrogus*, and the form of the vesicle is quite different and varies considerably in form as well as in size, but the most marked difference is that there is a firmer covering which appears to be in the nature of a well defined wall around the protoplasmic vesicle, while in *Artotrogus* there is only a protoplasmic membrane. Here the analogy ceases for zoospores are not formed. This cell is a germinal vesicle or proembryo, and from this proembryo arises the slender tube which pierces the cell of the prothallium and permits the parasite to enter. If the conidia are lying in an abundance of water they will germinate and produce a tube five to ten times the length of the diameter of the conidium. This I have several times observed, but in no such case have I observed the germ tube to enter a cell of the prothallium. Leitgeb

Explanation of Plate IV. *Completozia complens* Lohde.

Fig. 42 botryose cluster of plant body after being placed in water, the peripheral cells germinating and forming long tubes.

Fig. 43 plant body, some of the central cells forming resting spores, and some of the peripheral ones developing conidia.

Fig. 44 plant body in one cell of the host, the peripheral cells developing tubes which penetrate adjacent cells of the prothallium.

Fig. 45 two young plants in one cell of the host having entered from an adjacent cell, early stages in the branching and development of the botryose plant body are shown.

All figures drawn with aid of the camera lucida and magnified 30 times more than the scale. Scale, 1 millimeter.

states that in such cases which came under his observation the conidium only developed a short tube and then soon died.

The conidia possess a prominent apiculus which in development is directed toward and rests partly in the stalk of the sporangium. The sporangium develops from some of the superficial cells of the botryose body, but so far as I have examined from cells which are larger than the usual external cells. The cell begins growth in an upright position or away from the moisture and appears very much like an ordinary vegetative thread which is produced when the plant is immersed in water except that it is greater in diameter. When 60μ to 80μ in length the end becomes enlarged and the protoplasm collects into the forming sporangium. While the sporangium is forming the protoplasm is more coarsely granular at the base, while at the terminal portion it is more hyaline, giving the appearance of quite large and rather numerous vacuoles. When the spore is mature it is ejected with considerable force in much the same manner as the spores of the *Entomophthoræ*.

The aerial development of the sporangia instead of aquatic is in correspondence with the nonciliated condition of the conidia. One case which came under my observation shows clearly the necessity for the aerial development of the sporangia in the formation of the conidia in this plant. In mounting an affected prothallium in water for examination I discovered a partly formed sporangium which projected out into the cavity of an old and emptied ruptured cell. In the growing condition of the prothallia in this case they were somewhat crowded so that they stood more or less erect. The sporangium then in growing also in an erect position away from the moisture would be directed into the empty cell above. Placing this prothallium in a horizontal position on the glass slip in a small quantity of water would immerse the sporangium in the water, or partly so. All of the water was then drawn off except just a sufficient amount to prevent the prothallium and fungus from drying and the preparation was placed in a moist chamber in order that from time to time it might be examined to watch the development of the sporangium. This stage of the sporangium is represented in figure 43. No farther development of this sporangium took place. But just at the base of the stalk another one began to be thrown up in a position per-

pendicular to this prostrate one. As the new one increased in height the old one gradually lost the protoplasm both from the forming sporangium and the stalk. In the course of 4 to 5 hours the sporangium was mature and the conidium ejected, when the sporangium and stalk collapsed and remained as a flabby membrane attached to the wall of the old stalk and sporangium which was still in the water and which still remained intact.

The conidium is capable of germinating immediately when there is sufficient moisture and the behavior seems to be manifested in three different ways according to the amount of moisture, or in some cases perhaps according to the proximity of the host. If the spore is entirely immersed in water a long slender germ tube is put forth similar to the tube which is emitted from the terminal cells of the botryose body of a vegetatively mature plant. Where less water is present the conidium germinates by developing a germinal vesicle, or proembryo as described above.

From the inner face, the one lying next the prothallium cell, of the broader end of the proembryo, a minute tube is thrust out which pierces the cell wall of the host and grows out to the center of the cell lumen where in the ordinary way it enlarges into the first ovoid body of the new plant (fig's. 38, 40). In other cases probably, where there is still a less quantity of moisture, the tube from the germinating spore is directed upward or away from the host and becomes a sporangium with a very short stalk or only the short narrowed end of the sporangium which serves as a stalk. Before this conidium is ejected from this secondary sporangium if it be immersed in water, the protoplasm will grow out into a long slender germ tube. If it were only partially immersed it might as in the case of the primary sporangium noted develop a new sporangium. In the case of the primary sporangium which was immersed in water and which developed a new sporangium at the base of the old one, as described above, the base of the stalk was not entirely immersed.

As stated above the primary sporangia in the cases observed developed from some of the larger of the external cells of the cluster. In one case this took place while the inner cells were developing resting spores (fig. 34). It may be possible that the sporangia are always developed from somewhat larger and richer cells of the periphery but more likely others of the cells can

develop sporangia when the conditions of the environment, which have not all been determined, are such as to produce this tendency to fruit in the organism.

I have found the fungus in the prothallia of *Aspidium* (*Cyrtomium*) *falcatum*, *Pteris argyria* and *Pt. cretica*.

It was first described by Lohde²⁷ and was later more thoroughly studied by Leitgeb,²⁸ who grew it in a large number of fern prothallia.

A NEW CUTTING BED FUNGUS.

Volutella leucotricha Atkinson.

April 10th (1894) two cuttings, in the botanical conservatory, of carnations which were damping off were called to my attention. These were placed in a moist chamber expecting to obtain the sterile fungus or an *Artotrogus*. Two days later, 12th, the stems were well covered with a fungus which formed elevated stromata, whitish in color or with a slight tinge of flesh color. With a hand glass the stroma was seen to be surrounded by several setae, which, however, did not present at the time a dark color as is the case with the common carnation anthracnose, *Volutella dianthi* (Hals.). At the time it was supposed that this lack of color in the setae might be due to the growth. Sections of the stromata showed the structure of a *Volutella*, but the conidia were considerably smaller than those of *V. dianthi* and the setae were quite different in form as well as in color. They taper but little toward the free ends, are quite blunt at the ends and usually more times septate.

At my request Mr. R. H. Pettit, a student in my laboratory, made a separation of the fungus for me by the agarplate method. The first trial was successful and in a few days the colonies of the *Volutella* were visible to the unaided eye, the conidia having been kept watch of during the stage of germination and the formation of the colonies. The growth of the colonies is quite different from that of the *V. dianthi* as well as the development of the fruiting hyphae, and there was no longer any doubt that it was

²⁷ Ueber einige neue parasitische Pilze. Tagebl. d. 47 Vers. deutscher Naturf. u. Aertze, 203, 1874.

²⁸ Completoaria complens Lohde, ein in Farnprothallien schmarotzender Pilz. Sitzungsab. d. math. naturw. Klasse d. K. Akad. d. Wiss. LXXXIV, I, 288, 1881.

a different species from the *V. dianthi*, and the name *V. leucotricha* is here proposed for it.

Pure cultures were then started on bean and vetch stems and in a few days the characteristic stroma with the setae were developed in profusion on the surface of the stems. With the conidia from one of these cultures pure dilution cultures were made on April 20th. Instead of pouring a few drops of the first dilution into the second and from this into the third as I usually do with fungi having large conidia, the second and third dilutions were made by transferring with a double and twisted platinum needle. Plate number 1 and 2 were sufficiently separated for the study of colony characteristics and for photographing natural size. The colonies grow rather slowly and the plate No. 2 was ready for photographing on the 25th, and No. 3 on the 27th. In No. 2 the colonies were quite numerous and consequently rather small, from 4-6 mm. in diameter, while those in plate No. 3 where there were only 6 colonies were on the 27th 10 mm. in diameter. The colony steadily develops a thin and nearly circular web marked by numerous fine radiating lines which because of the exceeding thinness of the web are visible over the entire colony as it ages. There are quite regularly more dense radiating lines caused by the overlapping of certain radiating areas, and the margin shows a tendency to form roundish angles. The growth is quite sensitive to periodic changes in temperature which occur between night and day, as shown by the several concentric lines which are quite pronounced on the colony. At the center of the colony there is developed quite a compact stroma which is very much like that on a more solid substratum, like the stems of the vetch or bean. This stroma may be quite extensive and irregular in outline with a few outlying smaller and scattered ones, or there may be quite a large number of them at the center of the colony, the larger ones of course nearer the center and the smaller ones at the periphery. These individual stromata are so far like those developed in solid substrata, either in nature or culture tubes, that they are margined with the characteristic setae. A photograph of several of these growing in the agar in a Petrie dish is shown in fig. 52, plate VI, left upper corner. The photograph was taken from directly above and is magnified about 60 diameters.

In a few days after the appearance of the colonies the basidia

begin to develop. Some of them and probably the first ones are prostrate and wholly or partly immersed in the agar. They may be simple, or branched, when the branches may be opposite, or irregular, and in some cases the branches are assurgent, when most of them are thrown to one side. There is a strong tendency for the threads of the mycelium to assume a moniliform appearance by the swelling of the short cells thus producing a strong constriction at the septa. This tendency to a swelling of the cells of the mycelium is also shown to some extent in the basidia. Quite early many of the fruiting threads become erect and branch several times, the ultimate branches forming the basidia. The branches and the basidia are frequently opposite or whorled and when standing alone simulate very well the conidial fructification of a *Verticillium*. For some time the conidia are held in chains as they are developed successively on the same basidium. When moisture is sufficient, and this is usually the case in the Petrie dish, the capillarity of the film surrounding the conidia pulls them from the concatenate position and they are gathered into a globular head appearing as if they were developed in the form of a *Mucor*. Very soon at the center of the colony by the development of numerous fertile hyphae very closely, a true stroma is formed, and the conidia are held by capillarity in great masses upon the summit of the stroma.

April 24th a cell culture was prepared in a drop of nutrient agar at 5 P. M. On the following day the conidia were germinating and a group of them was photographed (46, Plate V. upper left corner). The spores here at this time were 4-5 μ in diameter. The germ tubes are quite sinuous and at this age (17 hours from time of sowing) were 15 μ to 25 μ long, and about 2 μ in diameter. In the germinating spores are a few, 3 to 5, small and very strongly refringent granules in the hyaline and homogenous protoplasm, and are quite well shown in the photomicrograph. On the following day when the culture was 40 hours old another photograph was taken (fig. 47). By this time many of the conidia showed the development of three tubes, and the tubes were now quite long. In some cases the hyphae coming in contact, anastomose, one of these conditions being shown in the photomicrograph. One day later several of the conidia showed still other tubes so that in time two to several tubes may arise from a single conidium. The anastomosing in



PLATE V.—*Volutella leucotricha* Atkinson.

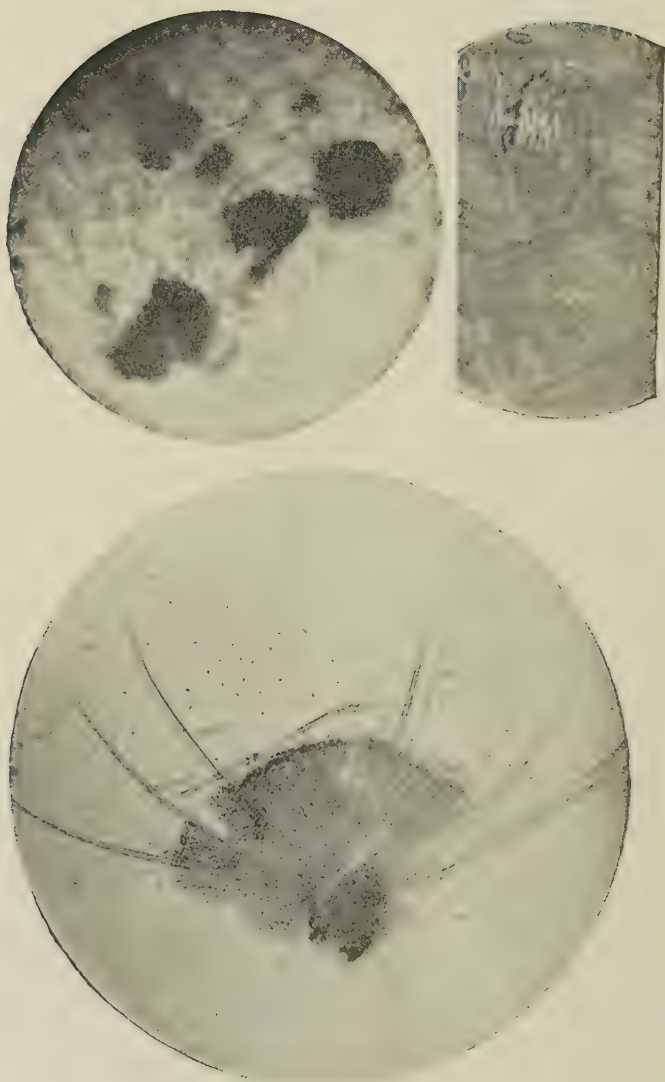


PLATE VI.—*Volutella leucotricha* Atkinson.

some cases is quite common. In this cell culture where the layer of nutrient agar was quite thin and the conidia numerous, fruiting did not take place very abundantly. In many cases the basidia are directly connected with the conidium, and in other and a majority of cases the basidia are developed from the hyphae at a variable distance from the conidium. The basidia under these circumstances are usually simple, terete and at the apex bear several conidia, which because of the rather large per cent. of water in the medium soon free themselves from the point of their origin and rest at one side. In a few cases the basidium is branched, or the fruiting hypha may bear lateral or opposite branches, and the terminal portion act as a basidium also. In this cell culture there was not the tendency for either the mycelium or the basidia to become swollen or enlarged. Two photomicrographs were taken of the conidium production in the cell culture, one showing the development of a basidium directly from the conidium (50 lower left) and one with two basidia near each other on a single thread of the mycelium (48 middle right).

In order to study the separate conidiophores, or fruiting hyphae recourse was had to the dilution culture, No. 1, in the Petrie dish. The conidia being so numerous in this dilution caused the development of numerous colonies in quite close proximity, and the fruiting was necessarily more scanty and a less tendency to the development of the stroma so characteristic of the fungus on solid substrata, or in the agar where they were not so crowded. There were therefore many scattered and independent fruiting hyphae or conidiophores. By placing a thin cover glass over portions of the plate these erect conidiophores were bent in a prostrate position, and the amount of moisture was sufficient to displace the greater amount of air so that the medium between the glass and the agar was nearly of the same density as the agar itself, and quite satisfactory photographs could be obtained when the subadjacent growth of mycelium was not too dense to interfere with the entrance of light, or to produce a hopeless confusion of threads which were not desired. Figs. 49, 51 and 54 represent some of the conditions of the conidiophores in this culture, which have been referred to above. (Figs. 46-51 and 54 were photographed at an amplification of about 600 diameters).

A portion of one of the fruiting stools which was teased out

from a culture on vetch stems was photographed with an amplification of 100 diameters and is shown in Fig. 53, Plate VI, lower figure. The preparation was mounted in water and the conidia which were so numerous that they would have clouded the preparation were mostly washed out. Quite a number, however, remained in the preparation, and show as minute oblong dark spots over the field of the photomicrograph. The fruiting stool is composed of numerous branched sporophores closely compacted together.

CANKER IN CUCUMBERS.

What is sometimes called canker in cucumbers has occurred during the two past winters in the horticultural houses of Cornell University. The appearance is that of a larger and deep ulcer in the stem at the surface of the ground. It occurs on plants of considerable size, on stems from 5 cm. to 1 cm. or more in diameter, the vines of which are several meters long. The ulcer has a dull brown color, the color of the external portion depending to some extent on the amount of soil which becomes worked into it. The tissues for some depth are soft and more or less putrid, dependent on the stage of the disease. It may advance so far as to cause the stem to rot off entirely, when of course the plant dies. In other cases the plant may not be ultimately killed but the ulcer has affected so deeply the vascular tissues as to interfere greatly with certain physiological functions of the plant. As the disease becomes serious the plants take on a sickly yellowish green color and become more or less limp. It soon runs its course, ending in death. During the month of December, 1894, sections of a diseased stem were placed in water and kept as described above for the seedling fungus, and in twenty-four hours a profuse growth of an *Artotrogus*, supposed to be the common *A. debaryanus* was developed. The species was at that time not accurately determined, and at the present writing there is none of the disease in the houses. The trouble is invited by keeping the soil around the stems in a too wet condition, just such conditions as favor the development of the seedling fungus. It is quite possible that another fungus to be described in a later paragraph may also have something to do with the etiology of the trouble.

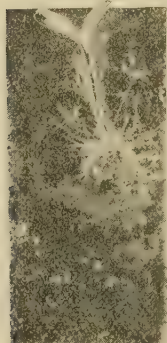
DAMPING OFF BY A STERILE FUNGUS.

Much of the trouble in the nature of damping off both in the forcing house and in the fields is caused by a fungus which has been under study at several different times during the last three years, but up to the present time has refused all the encouragement, which it has been possible from present experience to offer it with the hope of inducing it to develop some characteristic fruiting organs in order that its real nature and affinities might thus be made known. There are quite characteristic features of the mycelium and of certain sclerotoid bodies developed on the mycelium, and which with a little care serve to distinguish it from other known fungi.

I first observed it while studying the diseases of the cotton plant. (See Bull, Ala. Agr. Exp. Station, Dec. 1892.) In the cotton growing states it is a very frequent parasite on young cotton plants and produces a very large percentage, so far as my observation has gone, of what is known as "sore shin" in that section. The trouble is caused by the fungus growing first in the superficial tissues of the stem near the ground and disintegrating them before it passes to the deeper tissues, in other words the fungus never seems to penetrate far in the living tissues but "kills as it goes" and the tissues become brown, depressed and present the appearance of the plant having a deep and ugly ulcer at the surface of the ground. The fungus does not spread into the tissues either above or below the ulcer to any extent, but literally eats away at that point until it has severed the stem at the affected place or the plant has recovered from its effects. The plants do not seem to suffer seriously from the disease until the woody portion containing the vascular bundles is nearly or quite eaten away.

In the latter case all communication between the root and the aerial portion of the plants is cut off and of course the plant withers and dies. But frequently the stem may be eaten off so far that the plant has not sufficient strength in the remaining tissue at that point to support it and it will fall over, and perhaps if the disease does not progress any farther it may remain fresh and green for weeks, but it is rare that after this stage the plant recovers sufficient strength at that point to erect itself again. Frequently however when the stem is nearly eaten off the disease may be arrested and the plant completely recover from the effects.

During the winter of 1894-5, some bean plants in the horticultural forcing houses of Cornell University were affected by this disease and quite a number of them presented brown and quite deep ulcers on the stems of the surface of the ground. A few of the plants went so far as not to be able to stand. Some of the



55.—Sterile fungus grown on slide from seedling of *Centaurea candidissima*.

worst ones were pulled up, but others which were quite badly diseased remained in the bed and all gradually recovered completely. The plants were six to ten inches in height when the trouble was called to my attention. When the plants attain this size the disease cannot make such headway, but even very young plants will frequently recover from the effects.

It is more serious when it attacks smaller seedlings, as radishes, lettuce, etc. Egg plants and cabbages as well as others are known to be affected. Both the plants in seed beds in the forcing houses have been quite seriously affected by this fungus. Lettuce is frequently eaten off at the surface of the ground and the plants supported by others near may remain erect and fresh for several days. Gradually, however, if not quickly, they wither and fall when the fungus grows in the tissues farther as a saprophyte. If such plants be placed in a moist chamber, it is not necessary to place them in water, in a day or two there will be developed on the surrounding moist paper on which it is well to place the plants, a profuse growth of mycelium composed of whitish threads. To be sure that these threads are those of this fungus and not those of some mucor it will be necessary to have recourse to the microscope. The most characteristic peculiarity of the threads of the mycelium is to be found in connection with the branching. The freshly developed threads branch freely but not profusely, they are colorless, composed of elongated cells $9\ \mu$ – $11\ \mu$ in diameter and $100\ \mu$ – $200\ \mu$ in length. The protoplasm is finely granular and contains numerous small rounded vacuoles. The branches extend to an angle usually of between 30 and 60 degrees from the main hypha and very near the point of attachment are a little curved toward the point of growth of the same. At the point of attachment with the parent hypha the branch is considerably smaller

than either the diameter of the parent hypha or the main part of the branch, and the septum separating the protoplasm of the greater part of the branch from that of the parent hypha is situated some distance from the latter, usually $15\ \mu$ – $20\ \mu$ from the main thread. This portion of the branch then, the contents of which are continuous with those of the parent thread, is clavate in form. Species of *Botrytis* will occasionally be developed in diseased tissue of this kind, and sometimes develop phenomena of damping off similar to that produced by this fungus, though much more rarely, and the mycelium in its early stages cannot so far as I am able to tell be differentiated from this sterile fungus. But if a culture of the mycelium be made, in the course of a few days or in a week, if the mycelium be that of *Botrytis* the conidial stage or the clasping organs will be developed. But if it be that of this sterile fungus no such conidial stage will be developed.

Pure cultures of the fungus have been obtained at two different times. In the summer of 1892, from young cotton plants and again in February, 1895, from young lettuce plants which were damping off. It can quite easily be obtained in pure culture by transferring some of the mycelium grown in the air of a moist chamber, to some acidulated culture media. A very good medium is made by placing cuttings of bean stems, 7 to 8 centimeters long, in a culture tube and adding to this about 8 cc. of water and one drop of concentrated lactic acid. Several of these culture tubes should be prepared, and then sterilized in steam for two hours per day for three or four days in succession. The bean stems should project 2 to 4 centimeters above the liquid, and to the ends of these the mycelium can be transferred with a flamed platinum needle. Several transfers should be made and from portions of the mycelium which have been previously examined to be certain that mucors or other fungi are not present. Out of several transfers, if the growth in the moist chamber has been made with caution, a few pure cultures are quite likely to result.

Bacteria will be shut out by the acid in the medium, and if the culture is free from other fungi in a few days the mycelium will be visible as a silky white growth which spreads over the surface of the bean stems growing downward over them and also outward onto the surface of the glass tube. This growth continues to advance for several days with quite an even advance edge to the

weft. In the course of four or five days or one week, from the time that the mycelium is visible to the eye in the culture tube, there will appear first on the stems at certain points, and later on the surface of the glass tube, minute white powdery looking tufts on the mycelium. These are made up of closely and profusely branched threads, the branching sometimes presenting numerous and quite regular dichotomies, at other times quite irregular, and the terminal branches profusely lobed, the lobes standing in all directions and considerably more slender than the threads of the mycelium, and from 10μ to 20μ or more in length, occupying the distal portion of the branch for a distance from 20μ to 50μ . Another form of branching will also be present in which the closely set branches diverge at quite strong angles and are quite regularly constricted, presenting a moniliform appearance, and become eventually divided into short cells. These branches become more closely compacted and interwoven, forming rotund bodies at first white and quite small but eventually 2 to 4 millimeters in diameter and of a brown color. These bodies are probably sclerotia.

Upon the surface of these sclerotia are diverging threads with numerous moniliform cells which resemble chains of conidia. These are not true conidia since they do not easily become separated. By breaking down the sclerotia or by scraping the surface many of them become separated into chains of two or three cells or even become entirely separate. If placed in water, or in suitable medium, they will germinate, thus functioning like conidia.

The sclerotia have been kept for several months but in no case has any other stage of the fungus been developed from them.

At present it cannot be correlated with any known group of fungi but there are reasons for supposing that the sclerotia may be the resting stage of some hymenomycetous fungus. Frequently the threads become united into rope like strands and change to a brown color.

DAMPING OFF BY VARIOUS FUNGI.

Several fungi, probably quite a large number, produce phases of damping off at certain times while their evil effects are not confined to this peculiar class of injuries. *Phytophthora cactorum*

(L. et C.) Schroeter (*Phytophthora omnivora* deBary) was first discovered as the cause of decay of species of cactus in forcing houses. This fungus frequently destroys seedlings of trees, causing them to become brown and later to decay.

Several of the anthracnoses are known to produce genuine cases of damping off while their injury is by no means confined to this trouble. *Colletotrichum lindemuthianum* on bean seedlings is a good illustration of this, as Halsted²⁹ has already shown. The same author points out that a *Colletotrichum* on cuttings of albutilon, passiflora, clematis and jessamine causes them to damp off and in some houses ruins the bulk of the cuttings in the bed, while a *Gloeosporium* damps off rose cuttings.

Another anthracnose, *Colletotrichum gossypii* Southworth sometimes damps off seedling plants of cotton. Carnations are also affected in the same way by *Volutella dianthae* (Hals).

Halsted found a *Phyllosticta* in one case and in another case a *Septoria* growing in the stems of decaying chrysanthemums, and while this was the only fungus present it was not certainly determined as the cause of the trouble. According to Halsted bacteria also cause seedlings of cucumbers to damp off.

A species of *Botrytis* which is very common in forcing houses producing a variety of diseases of various plants frequently damps off leaves and twigs of cuttings or well rooted plants. When the houses are quite damp the fungus gains hold on the plant, probably in the axil of the leaf or branch, because the water is held at these points for a longer time, and once well seated in the tissue continues its work until the leaf or branch is rotted off. Leaves of begonias and branches of roses have been so damped off in the horticultural houses at Cornell University.

A careful inquiry would probably reveal a large number of fungi which at times produce diseases almost if not quite identical with damping off so far as external appearance goes.

TREATMENT.

In the treatment of this trouble especial attention must be given to the environment of the plants and those conditions which favor the rapid development of the parasites. These conditions are

²⁹4th Rept. N. Jr. Agr. Coll. Exp. Sta. 291, 1891.

known in most cases to be high temperature accompanied by a large moisture content of the soil, humid atmosphere, insufficient light and close apartments, and soil which has become thoroughly infested with the fungi by the development of the disease in plants growing in the same. Some excellent notes on the treatment of the disease by gardeners and horticulturists are given in the American Garden for 1890, by Meehan, Massey, Maynard, Watson, Lonsdale, Gardiner, and Bailey, and a short description of the potting bed fungus (*Artotrogus debaryanus*) by Seymour. The principal lines of treatment suggested there from the practical experience of the writers are as follows:

When cuttings are badly diseased they should be taken out, the soil removed, benches cleaned and fresh sand introduced, when only the sound cuttings should be reset. For cuttings is recommended a fairly cool house, and confined air should be avoided in all cases. As much sunlight as possible should be given as the plants will stand without wilting. When close atmosphere is necessary guard against too much moisture and keep an even temperature. The soil should be kept as free as possible from decaying vegetable matter. This is a very important matter, for several of the most troublesome of the parasites grow readily on such decaying vegetable matter and in many cases obtain such vigorous growth that they can readily attack a perfectly healthy plant which could resist the fungus if the vegetable matter had not been there to give it such a start. Soil which is dry beneath and wet on top as results from insufficient watering by a sprinkler favors the disease more than uniformity of moisture throughout the soil.

In seed beds use fresh sandy soil free from decaying matter. Avoid over watering especially in dull weather, shade in the middle part of the day only and keep temperature as low as the plants will stand.

If the seedlings are badly diseased it will be wise to discard them and start the bed anew. In the early stages however they can frequently be saved by loosening the soil to dry it, and placing the pots in sunny places at such times as they will not wilt. Some advocate sprinkling sulphur on the soil and in some cases sulphur at the rate of one to thirty is mixed in the soil before sowing with good effect. When the beds are badly infested

Humphrey³⁰ advocates the entire removal of the soil, whitewashing the beds, and the introduction of fresh soil.

In houses heated by steam if it were possible to have, without too great expense, a steam chest where the pots and seed pans which are used could be placed and the soil thoroughly steamed for several hours it could be sterilized, and the finer and more delicate seedlings be grown then with little danger if subsequent care was used to not introduce soil from the beds. In testing the virulence of the *Artotrogus debaryanus* (Hesse), and of the sterile fungus, several experiments have been made by steaming pots of earth, growing seedlings in them and then inoculating some of the seedlings with the fungus while other pots were kept as checks, and all were under like conditions with respect to moisture, temperature, etc. The seedlings which were not supplied with the fungus remained healthy while those supplied with the fungus were diseased and many killed outright (see frontispiece).

CONCLUSIONS.

Damping off is caused by the growth in the seedlings or cuttings of fungus parasites which themselves are plants but microscopic in size. The plants when affected frequently present a paler green color. The tissues become soft at the surface of the ground, the plant falls over and dies. No one fungus is concerned even in the soft rot of seedlings. In related cases the plant may show a brownish ulcer at the surface of the ground which frequently increases in size until the plant is severed at this point and then dies.

Too great a moisture content of the soil, air, high temperatures, close apartments, and insufficient light not only favor the rapid growth of the parasites but they also induce a weakly growth on the part of the seedling so that it cannot so readily resist the disease.

The parasites can grow and multiply on decaying vegetable matter which is in the soil.

When once in the soil they can remain alive for months even though the soil become dry or frozen.

Soil used in seed beds or cutting beds should be free from de-

³⁰ Mass. State Agr. Exp. Sta. Bull. 402, 1891.

caying vegetable matter or care should be used that the matter is thoroughly decomposed. Fresh sand is said to be the best for small seedlings.

Soil in which plants have once been diseased should be discarded if it cannot be sterilized by steam heat for several hours. Fresh soil free from vegetable matter should be introduced.

Water the soil thoroughly but not to saturation and do not water oftener than actually needed.

Keep the houses well lighted, well supplied with fresh air. Do not have high temperatures, keep as even a temperature as possible. When the disease first sets in stir the soil about the plants and do everything possible to dry the soil without killing the plants or raising the temperature, keep the temperature as low as the plants will bear. If this does not save them change the soil and clean the beds by whitewashing them.

When cuttings become seriously diseased change them to fresh soil, resetting only the perfectly healthy ones.

GEO. F. ATKINSON.

